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Deconstructed cat communities: quantifying the threat to felids from prey defaunation

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Abstract

Aim

Defaunation, the emptying of ecosystems of fauna, has been highlighted as a likely threat to the conservation of carnivores but the magnitude of this threat has yet to be quantified. We quantify the potential threat defaunation presents to wild felids.

Location

Global

Methods

For the 32 wild felids that feed primarily on mammals, we used 5330 prey records from 237 published sources to compile a new diet dataset, FelidDIET. This dataset was used to determine the relative importance of mammalian species as prey for each felid. These data were used to quantify the relationship between felid and prey species-richness, and to estimate the potential threat to wild felids from the loss of their prey.

Results

Our analyses reveal that models that include adjusted prey species-richness as a predictor of felid-richness out-perform those with less precise measures of prey-

richness (potential prey-richness and total mammal-richness). This is true both when examined collectively or when split into those felids that prey upon large-bodied prey and those that prey upon small-bodied prey. For seven felid species, including six large felids (over 15kg), 33% or more of their primary prey-species are threatened. Of most concern is the Sunda clouded leopard *Neofelis diardi*, for which 66.0% of its primary prey-species are threatened. In total, 57.6% of large felids' primary prey-species are threatened or declining, compared with 26.5% for small felids. Large felids are particularly vulnerable to primary prey decline in Indo-Malaya and East and Central Africa.

Main conclusions

Our findings indicate that imminent prey loss is likely to have substantial negative effects on large felids, many of which are already highly threatened. Considering the trophic cascades associated with large predators, the threat to large felids through the loss of prey diversity presents an ecosystem-scale threat.

Key words: Defaunation; Diet; Empty forest syndrome; Felids; Predator-prey interactions; Prey loss

(A) Introduction

Predators form a critically important component of a healthy ecosystem, and conservation focused upon these iconic species has the potential to benefit a wide array of lesser-known animals (Ripple *et al.*, 2014). However, large-bodied carnivores, in particular, are increasingly threatened by factors such as conflict with humans, habitat fragmentation and prey loss (Ray *et al.*, 2005; Ripple *et al.*, 2014). Prey loss is likely to be a crucial threat, as the diversity of mammal-dependent predators is strongly linked to the diversity of mammalian species; a relationship that is independent of the effects of climate or humans (Sandom *et al.*, 2013). A basis for this relationship is that foraging-resource diversity can provide a variety of niche spaces that allow consumers to diversify and coexist (Kissling *et al.*, 2007). Defaunation, for instance through poaching, can significantly affect prey populations (Geldmann *et al.*, 2013), leading to 'empty forest' syndrome (Harrison, 2011).

Understanding the importance of different threats is valuable for developing future conservation strategies across all taxa. For felids, issues such as conflict with humans

have received significant attention (Woodroffe *et al.*, 2005; Inskip & Zimmermann, 2009; Loveridge *et al.*, 2010), but there has been less focus on quantifying the generalised significance of prey loss (Ripple *et al.*, 2014). Mammal decline is a global issue with almost a third of all mammal species classified as declining (30.1%, 1651), and 17.9% (985) as both declining and threatened (International Union for Conservation of Nature (IUCN) 2013). These declines are likely to pose a particular threat to felids, which are primarily specialist carnivores meaning they are more dependent upon mammalian prey than any other non-monospecific mammal family (Kissling *et al.*, 2014). This threat to prey-species is a rarely examined, yet, potentially major risk for the long-term persistence of felids and other carnivores.

In light of current dramatic declines in mammal diversity and abundance (Barnosky *et al.*, 2011), termed ‘anthropogenic defaunation’ (Dirzo *et al.*, 2014), we explore the degree to which a potential loss of prey-species presents a threat to wild felids. First, we collate felid diet data and use these data to estimate the primary prey of each mammal-dependent felid across their range. We then take a macro-scale perspective and explore hypothetical scenarios that simulate the impact on felid-richness of the functional extinction of all currently threatened (Vulnerable or worse) or declining mammal species, as classified by the IUCN (2013). Our results provide valuable insights into the security of the prey base for wild felids, and highlight the potential risks that defaunation presents to felid conservation.

(A) Methods

We created a new dataset of felid diets (FelidDIET), collated from the published literature for the 32 felids that primarily hunt mammals. FelidDIET includes data on: 1) species and taxonomic groups (genera, family, order) which have been recorded as prey; 2) a quantitative or qualitative record of dietary importance of each recorded prey; 3) where the record was made; and, 4) the data collection method that was used (Appendix 1; Fig. S1; Table S1). The species-, genus-, family- and order-level prey data stored in FelidDIET were then used to estimate the relative importance of each mammalian species (excluding Carnivora) in each felid’s range as prey to create a secondary dataset called FelidDIET-Extrapolated (Appendix 2; Fig. S1; Table S2; see supplementary material for a full account of the construction of both datasets and testing of FelidDIET-Extrapolated). In FelidDIET-Extrapolated, all terrestrial

mammal species within each felid's range were assigned to one of four dietary importance categories: primary prey (Category 1); secondary prey (2); occasional prey (3); or, non-prey (4) (Fig. S1; Table S3). Prey were classified in terms of their dietary importance using published quantitative data, or from published descriptions following Kissling et al. (2014). Where quantitative diet data were available, primary prey were prey items or groups that appeared in $\geq 20\%$ of diet samples, secondary prey appeared in $\geq 5\%$ and $< 20\%$ of diet samples, and occasional prey appeared in $< 5\%$ of the diet samples. Sensitivity tests were carried out to investigate the impact of increasing the primary prey threshold to 25% and reducing it to 15%. Only primary prey was analysed and quantitative diet data based on fewer than 20 samples were excluded from the analysis. Where no indication of prey importance was available, the prey item was classified according to the quality of diet data available for that felid. Diet data quality within FelidDIET were assessed by scoring each felid according to the number of geographical site locations and samples (e.g. scats) for which quantitative prey data were available (see supplementary methods). For felids with 'High' or 'Very High' data quality (Table S4), the 24 prey records in FelidDIET that did not include a description of importance were categorised as secondary prey. Prey records for felids with 'Poor' or 'Very Poor' data quality (Table S4) that did not include a description of importance were categorised as primary prey on the basis that this represents the best available data of prey preference for these felids.

To explore the robustness of the primary prey estimations, for each felid we: 1) mapped the number of quantitative dietary samples available per country across the felid's range to determine the spatial extent of diet data (Fig. S2a); 2) mapped primary prey-richness recorded at either species or genus level (Fig. S2b), and prey-richness recorded at either species or genus, family and order level (Fig. S2c), and plotted the two against each other (Fig. S2d) to identify the implications of including prey data at a low taxonomic resolution; and, 3) plotted how primary prey species-richness increased, and how maximum and minimum prey body mass increased and decreased respectively, when increasing the number of published data sources included (Fig. S2e).

(B) Distinguishing between large and small felids

Carbone et al. (1999) reported that large mammalian predators, including felids, are energetically constrained to rely on large prey-species, while small predators are morphologically constrained to rely on smaller-bodied prey. For the purpose of this analysis we classified felids into two guilds, those that primarily predate large-bodied prey (referred to as large felids) and those that primarily predate small-bodied prey (small felids). We followed Carbone's et al. (2007) threshold of 15kg to identify large felids (including: tiger *Panthera tigris*, lion *Panthera leo*, jaguar *Panthera onca*, leopard *Panthera pardus*, puma *Puma concolor*, cheetah *Acinonyx jubatus*, snow leopard *Panthera uncia*, clouded leopard *Neofelis nebulosa*, Sunda clouded leopard *Neofelis diardi* and Eurasian lynx *Lynx lynx*) and checked this relationship held for our data in this analysis. A linear model was used to assess the relationship between felid mass and primary prey mass. Both masses were log-transformed.

(B) Mapping

We used global species distribution maps for the 32 felids and 4045 terrestrial mammal species, excluding Carnivora, that overlapped the felids' ranges (IUCN, 2013). Polygonal range maps were converted to rasters on a Behrmann projection, approximately equivalent to a 2-degree cell resolution at the equator (a cylindrical equal area projection, cell resolution = 193.0 km). A species was assumed to be present in a cell if any part of the cell was covered by the species' extant range polygon. We excluded Australia and Antarctica as they have no indigenous felids and would generate zero-inflated data. Grid cells with <50% land area and cells missing forest cover data were also excluded, resulting in 3250 cells in our analysis. All data handling and plotting was performed using R statistical program, version 3.1.2 (R Core Development Team, 2014), using the raster (Hijmans, 2015), rgdal (Bivand *et al.*, 2015), and maptools packages (Bivand & Lewin-Koh, 2015).

(B) Data Analysis

(C) Predicting current felid-richness

To assess the performance of prey-richness as a predictor of felid-richness two measures of prey-richness were compared with terrestrial mammal-richness. The first measure of grid cell prey-richness was a measure of the felids' primary prey-species, regardless of whether the felid was present in that cell or not. This measure is referred

to as ‘potential’ prey-richness, reflecting the availability of prey if all felids could disperse everywhere. The second measure of prey-richness only included the primary prey of the felids assumed to be in each cell; this measure is referred to as ‘adjusted’ prey-richness.

Felid species-richness was analysed using General Linear Models (GLMs) with a poisson distribution and log link function, first for all felid species-richness and then separately for large and small felids. Explanatory variables included an estimate of prey-richness (adjusted prey, potential prey or all terrestrial mammal-richness), as well as biogeographic realm (Fig. S4; Qian, 2010), human footprint (Sanderson *et al.*, 2002), normalized difference vegetation index (NDVI; <http://edit.csic.es/Soil-Vegetation-LandCover.html>) and forest cover (from global estimates of tree cover from the MODerate-resolution Imaging Spectroradiometer (MODIS), using the vegetation continuous field version 4 (Hansen *et al.*, 2010). Combinations of the explanatory variables were used to build 18 candidate models of increasing complexity (see Table 1 and supplementary materials for an explanation of interaction selections) which were compared using an Information Theoretic approach (using the ‘MuMIn’ package (Bartoń, 2015). We ranked the candidate models by their second-order Akaike Information Criterion (AIC_C) values and Akaike weights (ω_i), which represents the strength of evidence for each candidate model being best model of those fitted to the data. AIC considers both model fit and complexity, and finds models that most parsimoniously represent the strongest relationships. Models with the highest AIC weight are those most likely given the data, and an Akaike weight > 0.9 indicates there is a single best model (Burnham and Anderson 2002). If Akaike weights indicate there is no single best model, this is an indication of uncertainty in model selection. We used multi-model inference to calculate model-averaged parameter estimates of the strength of the relationship between each explanatory variable and the response. To assess the degree of spatial autocorrelation (SAC), we computed correlograms of the best-fit GLM residuals using the ‘ncf’ package (Bjornstad, 2012), with distance classes of 1000 km. None of the models indicated substantial SAC (Fig. S4) so we used the GLM models in the analysis.

(C) Predicting future felid-richness under a defaunation scenario

To assess how well the best-fit models explain large and small felid-richness, observed felid-richness was subtracted from predicted felid-richness and plotted. Values of zero indicate the model predicts as many felids as observed, while positive numbers indicate the model predicts a higher felid-richness than observed and negative numbers indicate lower richness than observed. These models were then used to predict felid species-richness firstly under a scenario where all threatened prey-species were removed from ‘adjusted’ primary prey-richness, and secondly with threatened or declining prey-species removed. To estimate the potential reduction in felid-richness as a result of defaunation per cell, predicted felid-richness using only non-threatened primary prey-richness was subtracted from predicted felid-richness using observed primary prey-richness. This process was then repeated, replacing the predicted felid richness generated using the non-threatened primary prey-richness variable with the predicted felid richness generated from the non-threatened and non-declining primary prey-richness. Analyses were conducted on datasets for large and small felids separately. The maximum value for predicted felid species-richness was limited to the maximum number of felids present in that biogeographic realm.

(C) Which felids are most at risk?

In regions where felid-richness is predicted to decline, the weakest competitors within the felid community are the most likely to be lost. We identified the weakest competitors as the felids that have low prey-richness or high dietary overlap with other felids, and with a highly threatened prey resource. To assess the degree to which each felid is threatened by a loss of prey species-richness we estimated each felid’s relative resistance to defaunation over its range. Each felid’s resistance to defaunation was estimated for each grid cell by dividing the number of its primary prey-species in the cell by the mean number of felids competing for each prey-species and multiplying the result by the proportion of its prey-species that are not threatened or declining in that given cell (Eq. 1). Lower numbers indicate felids with an estimated lower resistance to defaunation. To obtain a standard score of each felid’s resistance to defaunation, the mean resistance score was calculated across the cells within each felid’s range. Competition was calculated per felid per cell by counting the number of other felids that occur in the cell that share each of the felid-in-question’s primary prey, and calculating the mean over all prey-species.

Equation 1: Resistance

$$= \frac{\text{prey richness}}{\text{competition for prey}} \times \text{proportion of prey not threatened or declining}$$

(A) Results

(B) Felid to prey body mass relationship

Felid body mass was positively correlated with primary prey body mass (Fig. S5, Tables S5 & S6). This result supports the use of the 15kg value for identifying large and small felids, with large felids being largely restricted to large prey and small felids to small prey (Fig. S6). Plotting the felid primary prey mass reveals that caracal (*Caracal caracal*; the largest small felid) predated a broader range of primary prey masses, including more smaller-bodied prey than the smallest large felid, Eurasian lynx (Fig. S6 a,b). Furthermore, while Eurasian lynx is the largest felid over most of its range (67%), caracal is the largest felid over only 26% of its range.

(B) Felid-Prey richness relationships

Maps of felid-richness, mammal-richness, potential primary prey-richness and adjusted primary prey-richness for both large and small felids show similar patterns as subsets of biodiversity follow the global spatial pattern of species-richness (Fig. 1). The information-theoretic approach revealed those models that included the terms for adjusted primary prey-richness, as opposed to other measures of prey-richness (mammal species-richness or potential primary prey-richness), were by far the best supported models to explain all, large and small felid-richness (Table 1). The best models also included biogeographic realm, forest cover, human footprint, NDVI and interaction terms. Adjusted prey-richness was the most important individual predictor of felid-richness for all and large felids, and the second most important after NDVI for small felids (Table 2).

(B) Defaunation

Of the 2,534 mammal species recorded to be primary prey of felids, 21.7% are threatened, and 13.3% are declining but not yet threatened. For seven of the 32 felid

species, 30% or more of their primary prey-species are threatened (Table 3). Of most concern is the Sunda clouded leopard, for which 66.0% of its primary prey-species are threatened. For eight felids, 50% or more of their prey base are threatened or declining (Table 3), including the Iberian lynx *Lynx pardinus* that only has one primary prey-species, European rabbit *Oryctolagus cuniculus*, which is declining. The mean proportion of primary prey threatened or declining is 57.6% for large felids and 26.5% for small felids.

The number of primary prey-species that are threatened or declining varies geographically, and the pattern is not consistent between the large and small felids (Fig. 2). In Indo-Malaya the mean proportion of primary prey of large felids that are threatened per cell is 34.3%, which rises to 58.8% when including both threatened or declining prey-species. The mean proportion of large felids' primary prey that are threatened is also high in the Afrotropics (21.2%), rising to 42.1% when also including declining prey (Fig. 2a). In the Palearctic, threatened primary prey account for 15.8% of all primary prey, but rises to 32.5% when including declining species. Only in the Nearctic are the proportions of threatened or declining primary prey of large felids low (0.1% threatened and 9.5% threatened or declining). The proportions of primary prey of the small felids are by contrast relatively low overall, with the highest mean proportion of threatened prey in the Afrotropics (6.9%) and threatened or declining prey in Indo-Malaya (25.3%; Fig. 2c,d).

(B) The threat defauna presents to felids

The models used to predict large felid species-richness with adjusted primary prey species-richness predicted the correct number of large felids in a cell 69.8% of the time (Fig. 3a). The regions that recorded the greatest discrepancy between observed and predicted felid-richness were central and eastern Asia. Using the models to predict felid-richness, having removed threatened large felid prey, suggests that one or more large felids will be at risk from defauna across an area of approximately 15.2 million km² (409 cells; Fig. 3c). The regions under greatest threat are in south-eastern Asia, Indo-Malaya, central and southern Africa and a few areas of central South America. If declining prey-species are also removed, large felids in a further ~14.6 million km² (393 cells) would be at risk, particularly in South America, East Africa and North America (Fig. 3e). In total, our models suggest at least one large

felid in 20.8% of cells with large felids (~2.5 million km², 678 cells) is at risk from defaunation.

Models used to predict small felid species-richness with adjusted primary prey species-richness predicted the correct number of small felid species in a cell just over half (54.0%) of the time (Fig. 3b). The model predicts there is sufficient prey-richness to support more small felid species than currently exist in areas of central and northern Africa, central Asia and patches of South and North America (Fig. 3b). The model also predicts that current small felid-richness is greater than would be expected for prey-richness in northern-central Africa, the Iberian Peninsula, some parts of South and North America, but particularly in the Middle-East, Kazakhstan and India. Using the models to predict felid-richness, having removed threatened small felid prey, suggests that one or more small felids will be at risk from defaunation over approximately 4.7 million km² (125 cells, Fig. 3d). If prey-species that are recorded to be declining are also removed, small felids across a further 11.5 million km² would be at risk (310 cells; Fig. 3f). In total small felids in 13.4% of cells with small felids 435 cells (~16.2 million km²) are at risk from defaunation.

(B) Threat to particular felids from defaunation

Defaunation threatens a wide variety of large and small felids (Fig. 4, Fig. S7). Of the large felids, snow leopard and tiger record the lowest mean resistance scores (Table 3). Cheetah, lynx, and Sunda clouded leopard score the next lowest mean resistance scores for the large felids. Iberian lynx records a mean resistance score of 0, because its only primary prey, European rabbit, is declining. Kodkod *Leopardus guigna*, and Canadian lynx *Lynx canadensis* also record very low mean resistance scores. Both of these species have very low primary prey-richness (Fig. S2).

The vulnerability of large felids to a threatened and declining prey base varies between felid and also within the range of individual felids (Fig. S6). For example, the tiger has low primary prey-richness over its range (Fig. S2), and as much as 88.9% of its primary prey-species are threatened or declining in some areas (Fig. 4). Both leopard and cheetah face substantial risk from minimal primary prey-richness in northern Africa and the Middle-East (Fig. S2). The primary prey of leopard are particularly threatened or declining in Indo-Malaya, while 100% of cheetah's primary

prey is threatened or declining in northern Africa (Fig. 4). The Sunda clouded leopard records a relatively large prey base compared to the tiger, but at least 65.2% of these prey-species are threatened in each of the cells Sunda clouded leopard occupies. Mean competition for primary prey-species is typically greater in small felids than it is in large felids (Fig. S8). The greatest average competition for prey-species in a single cell is 5.8, for the jaguarundi *Puma yagouaroundi*. South America has particularly high average competition for prey-species among small felids.

(A) Discussion

Having tested a variety of measures of prey-richness, we find the most precise of those measures to be the best predictor of felid-richness at macroscales. The relationship between large felid-richness and the diversity of their prey was particularly strong. Thus, the database FelidDIET-Extrapolated proves to be a useful representation of felid primary prey. This resource offers macro-ecologists insight into community structure and conservationists the opportunity to identify which mammals are likely to be particularly important in under-pinning the protection of felid communities (Fig. S2; Appendix 2). For example, we recommend further consideration of prey loss as a potential threat to *L. guigna* and *N. nebulosa*. The IUCN lists the major threats of *L. guigna* as habitat loss and fragmentation, and direct persecution by humans, whilst for *N. nebulosa* the major threats are deforestation and hunting, while prey decline is not listed as a potential threat to these felids. However, we find their resistance scores to defaunation to be similar to other felids where prey decline is a listed threat, and we find 50% or more of the felids' prey to be declining or threatened. Conversely, *Otocolobus manul* has a high defaunation resistance score but loss of prey has been identified a threat by the IUCN because of widespread poisoning of rodents within its range (Table 3).

The importance of adjusted primary prey-richness in explaining felid-richness in our models, particularly for large felids, emphasises the importance of maintaining a broad assemblage of prey-species for preserving felid communities. Ominously, in terms of biodiversity conservation, many of the felids' primary prey-species are threatened or are declining in range and/or abundance and so becoming functionally less available as prey for felids. We predict that if declining prey-richness continues,

it could threaten large and small felids in all five biogeographic realms studied and as many as five large and four small felids in a single cell in some regions of Indo-Malaya and Asia (Fig. 3e,f), assuming that there is no significant switching from primary prey to secondary or even current non-prey species.

We found FelidDIET-Extrapolated to be a useful resource in understanding the trophic relationships between felids and their mammalian prey. However, understanding the importance of varying diet data quality for the felids is important. One measure of diet data quality is to consider the taxonomic level at which the diet data were collected. Only using species- and genera-specific prey data to estimate prey-richness ensures a high probability that these prey-species are important. Including family- and order-specific species increases the probability of including species that should not be considered primary prey-species but reduces the probability of erroneously excluding prey-species in regions with little or no diet data. We investigated the relationship between species- and genera-specific primary prey-richness and primary prey-richness recorded at all taxonomic resolutions (Fig. S2). There were clear differences between different groups of felids. Tiger, lion, jaguar, cheetah, snow leopard, and sand cat *Felis margarita* all recorded similar primary prey-richness regardless of which taxonomic level of prey data were included. This indicates that, at least for the felids with Very High data quality in this group, there is strong support that we have a reliable estimation of their diet across their range. The sand cat is an anomaly in this group as it is the only felid with Poor data quality. It is likely this pattern was observed because the low mammal diversity across the sand cat's range means that there are few alternative potential mammal prey-species available to it. Leopard, clouded leopard, Sunda clouded leopard, ocelot *Leopardus pardalis*, Asian golden cat *Pardofelis temmincki*, African golden cat *Caracal aurata*, bobcat *Lynx rufus*, jaguarundi, jungle cat *Felis chaus*, Pallas's cat *Otocolobus manul*, margay *Leopardus wiedii*, oncilla *Leopardus tigrinus*, and rusty-spotted cat *Prionailurus rubiginosus* all have similar geographical patterns of prey-richness across the measures of primary prey-richness, but adding family- and order-specific species considerably increases primary prey-richness (Fig. S2). These diet data suggest these species are highly generalist predators, all capable of utilising relatively small mammals as primary prey. The extent to which family- and order-specific prey-species are indeed primary prey is difficult to determine. This is because data

collected at family or order resolution can include species with a diverse range of life histories some of which are likely to make particular species within the taxonomic group unsuitable as primary prey. Data on, for example, habitat preference, activity period, foraging strategies, and predator defence mechanisms for all mammals would improve our ability to predict these felid's prey more precisely. The data stored in FelidDIET clearly suggests Iberian lynx and Canadian lynx are specialists targeting a single prey-species. Kodkod, and black-footed cat *Felis nigripes* both record very low prey-richness across all measures of prey-richness but whether they are specialist predators or whether their diet data is deficient is unclear. Finally, puma, Eurasian lynx, caracal, serval *Leptailurus serval*, Andean mountain cat *Leopardus jacobita*, wild cat *Felis silvestris*, pampas cat *Leopardus colocolo*, Geoffroy's cat *Leopardus geoffroyi* and leopard cat *Prionailurus bengalensis* record differing geographical patterns of prey-richness when family- and order-specific species are added and including these prey-species considerably increases total prey-richness. For all of these felids, adding the family- and order-specific diet data may be correcting bias towards higher prey-richness in regions of greater data collection effort (e.g. wild cat which has high sampling effort and high species- and genera-specific prey-richness in Europe, but high total prey-richness in sub-Saharan Africa; Fig. S2a,b,c). However, as with the group including the leopard, the diet data suggests these felids are generalist predators capable of utilising a wide variety of prey-species. It will be interesting to see how adding data to FelidDIET will change FelidDIET-Extrapolated. The increased focus on trait-based analyses to understand ecosystem function (Kissling *et al.*, 2009; Greve *et al.*, 2012; Kissling *et al.*, 2014; Wilman *et al.*, 2014) should encourage greater effort to record a predator's prey-species over the entirety of their range.

The consistent felid prey-richness relationship observed in both large and small felid guilds (Fig. 1; Table 1) and the strong relationship between the body masses of felids and their primary prey (Figs. 1 & S3) indicates niche separation generated by variation in prey-species is likely to be important in predator community assembly, speciation and persistence (Hutchinson, 1959; Chesson, 2000; Sinclair *et al.*, 2003; Kissling *et al.*, 2007). Thus, maintaining prey-species diversity will be important for maintaining felid diversity and evolutionary potential. Worryingly, our results indicate large felid prey in particular is threatened and in decline.

Defaunation is a considerable and growing threat to wildlife conservation, often driven by people's dependence on bush meat for income (Bowen-Jones *et al.*, 2003) or nutrition (Fa *et al.*, 2003). Evidence suggests bush meat hunting can drive considerable declines in species populations and large-bodied mammals are often most at risk (Lindsey *et al.*, 2013). Our results are consistent with this, as we found large felids prey are more at risk from defaunation compared to small felids. Field evidence from the Congo Basin has demonstrated that defaunation, in this case caused by high human hunting intensity for bush meat, has led to the exclusion of leopard in some regions (Henschel *et al.*, 2011). Interestingly, Henschel *et al.* also demonstrate that where leopards persist they switch to smaller prey, what we would consider to be secondary prey, at higher human hunting intensities, presumably thereby exposing smaller felids to more intense competition. It is important to note that this analysis focuses on the potential declines that felids may face as a result of declines in their current primary prey-species. Considering the potential for felids to switch to secondary prey, as per the leopard example, was beyond the scope of this analysis but bears further consideration.

While considerable attention has been paid to the threat of defaunation in tropical forests (Fa & Brown, 2009; Abernethy *et al.*, 2013), other habitats are also threatened including savanna (Lindsey *et al.*, 2013) and mountains (Topp-Jorgensen *et al.*, 2009). South-east Asia and Eastern and Southern Africa are the regions where large felids are most vulnerable to defaunation, as a result of high numbers of threatened or declining primary prey. Interestingly, our models suggest that in much of Indonesia observed prey-richness should be able to support a greater diversity of large felids. However, our models also suggest that the loss of both threatened and declining prey would still cause the loss of at least one large felid over large areas of this region (Fig. 3).

The model predicting small felid-richness with current adjusted prey-richness did not perform as well as the large felid model, with a correct number of small felids predicted in a cell only 54.0% of the time. We hypothesize that smaller mammals are more similar to each other than larger ones, resulting in less niche separation driven by prey differentiation than in large felids. In support of this, we found that NDVI

was a more important predictor of small felid-richness compared to prey-richness, contrary to the large felid model. Furthermore, smaller felids could have the added pressure of strong top-down competition from larger predators, higher proportion of non-mammalian prey, intra-guild competition and greater limits to dispersal that could drive speciation and alter community assembly. Alternatively, this result might be a factor of the poorer quality of prey data recorded for the small felids resulting in more generalised primary prey data.

The observation of trophic cascades as the result of the loss of large predators has highlighted the ecosystem level effects of large predators (Estes *et al.*, 2011; Ripple *et al.*, 2014). Loss of prey may trigger ecosystem effects that first climb the trophic pyramid by threatening felid survival through reducing prey-richness, followed by cascading effects as a result of the loss of predators no longer interacting with their remaining prey-species (Ripple & Beschta, 2007; Manning *et al.*, 2009; Oriol-Cotterill *et al.*, 2015). Equally, the greater threat posed to large felids may cause them to be lost from systems before smaller felids with the potential for meso-predator release with negative consequences for their prey-species (Ripple *et al.*, 2014).

We provide evidence that large felids are at greater risk from defaunation than are small felids. However, knock-on impacts of declining large-bodied prey could increase competition between large and small felids. The most ominous situations prevail for large felids in Africa, particularly in the east and south, and Asia, particularly in the southeast. Our study highlights the potentially catastrophic consequences for carnivores, particularly the iconic big cats, of the very high proportion of threatened or declining large herbivore populations.

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Biosketch

Christopher J. Sandom is a Lecturer at the University of Sussex. His research is focused on trophic cascades, predator-prey interactions, restoration ecology, and rewilding. He is particularly interested in exploring how trophic cascades can be restored to improve biodiversity conservation and deliver a net positive impact on nature.

Author contributions: CJS conceived the idea. CJS, DB, AD, AEH, EAM, DWM designed the study. CJS, JW, and AEH collected the data. CJS and AEH conducted the analysis. CJS led the writing with input from all co-authors.

Tables

Table 1: Model AIC values using different mammal-richness measures to predict all, large and small felid-richness.

All Felids					
Model rank	Variables in model	df	AICc	ΔAIC_c	Weight (ω_i)
1	1+2+4+5+6+8+11+12+15+16	17	10076.01	0	1
2	1+2+4+5+6+11+12+15+16	13	10196.14	120.13	0
3	2+4+5+6+11+12+15+16	9	10481.65	405.64	0
4	1+3+4+5+6+9+13+14+15+16	17	10552.85	476.84	0
5	15+16	13	10610.19	534.18	0
6	2+5+6+11+12+16	7	10651.01	575.00	0
7	1+4+5+6+7+10+15+16+17+18	17	10680.50	604.49	0
8	2+5+6+11+12	6	10718.77	642.76	0
9	1+4+5+6+7+15+16+17+18	13	10724.88	648.87	0
10	2+6+12	4	10781.91	705.90	0
11	3+4+5+6+13+14+15+16	9	10959.30	883.29	0
12	4+5+6+7+15+16+17+18	9	11237.28	1161.27	0
13	3+5+6+13+14+16	7	11294.96	1218.95	0
14	3+5+6+13+14	6	11388.57	1312.56	0
15	3+6+14	4	11465.89	1389.88	0
16	5+6+7+16+17+18	7	11730.47	1654.46	0
17	5+6+7+17+18	6	11864.69	1788.68	0
18	6+7+18	4	11964.51	1888.50	0

Large Felids					
Model rank	Variables in model	df	AICc	ΔAIC_c	Weight (ω_i)
1	1+2+4+5+6+8+11+12+15	17	6586.03	0.00	1
2	1+2+4+5+6+11+12+15	13	6735.79	149.76	0

	14+15				
	2+4+5+6+11+12+14				
3	+15	9	6939.68	353.65	0
4	2+5+6+11+12+15	7	6942.63	356.60	0
5	2+5+6+11+12	6	6960.54	374.51	0
6	02+06+12	4	6975.47	389.43	0
	1+4+5+6+3+9+14+1				
7	5+16+14	17	7081.81	495.78	0
	1+4+5+6+7+10+14+				
8	15+13+18	17	7099.17	513.14	0
	1+4+5+6+3+14+15+				
9	16+14	13	7183.50	597.47	0
	1+4+5+6+7+14+15+				
10	13+18	13	7222.20	636.17	0
	4+5+6+3+14+15+16				
11	+14	9	7432.68	846.65	0
12	5+6+3+15+16+14	7	7439.54	853.51	0
13	5+6+3+16+14	6	7463.85	877.82	0
14	06+03+14	4	7473.71	887.68	0
15	5+6+7+15+13+18	7	7577.31	991.28	0
	4+5+6+7+14+15+13				
16	+18	9	7577.56	991.53	0
				1003.2	
17	5+6+7+13+18	6	7589.29	6	0
				1033.7	
18	6+7+18	4	7619.78	5	0

Small felids					
Model rank	Variables in model	df	AICc	ΔAICc	Weight (wi)
	1+2+4+5+6+8+11+1				
1	2+14+15	17	8280.78	0.00	1
	1+2+4+5+6+11+12+				
2	14+15	13	8506.88	226.10	0
	1+4+5+6+3+9+14+1				
3	5+17+14	17	8765.16	484.37	0
	2+4+5+6+11+12+14				
4	+15	9	8782.35	501.57	0
	1+4+5+6+7+10+14+				
5	15+16+13	17	8821.23	540.45	0
	1+4+5+6+3+14+15+				
6	17+14	13	8832.67	551.89	0
	1+4+5+6+7+14+15+				
7	16+13	13	8857.83	577.05	0
	4+5+6+3+14+15+17				
8	+14	9	9195.72	914.94	0
9	2+5+6+11+12+15	7	9223.56	942.78	0
10	4+5+6+7+14+15+16	9	9263.57	982.79	0

	+13			1005.3	
11	2+5+6+11+12	6	9286.14	5	0
				1074.1	
12	2+6+12	4	9354.89	1	0
				1800.3	
13	5+6+7+15+16+13	7	10081.13	5	0
				1943.4	
14	5+6+7+16+13	6	10224.22	4	0
				2025.3	
15	6+7+13	4	10306.11	2	0
				1633.8	
16	5+6+3+15+17+14	7	9914.64	6	0
				1756.4	
17	5+6+3+17+14	6	10037.25	6	0
				1818.9	
18	6+3+14	4	10099.76	7	0

Key to variables:

Variables		Definition
Realm	1	Biogeographic realm
ExpPrey	2	Prey actually exploited by present
FelidPrey	3	Prey that could be exploited if felids were everywhere
Forest	4	Forest cover
Human	5	Human Impact
NDVI	6	NDVI
Mammals	7	Total Mammal-richness (no bats)
Realm:ExpPrey	8	
Realm:FelidPrey	9	
Realm:Mammals	10	
ExpPrey:Human	11	
ExpPrey:NDVI	12	
FelidPrey:Human	13	
FelidPrey:NDVI	14	
Forest:NDVI	15	
Human:NDVI	16	
Human:Mammals	17	
NDVI:Mammals	18	

Table 2:

Coefficients from the best general linear model as identified in Table 1 for all, large and small felids. Key to variables is available in Table 1.

All Felids	Estimate	Std. Error	z value	P
(Intercept)	1.231	0.033	37.417	<0.001
ExpPrey	0.716	0.055	12.978	<0.001
NDVI	0.169	0.065	2.604	0.009
Human	-0.154	0.035	-4.337	<0.001
Forest	-0.353	0.054	-6.509	<0.001
Indo-Malaya	0.250	0.051	4.937	<0.001
Nearctic	-0.552	0.048	-11.534	<0.001
Neotropics	0.189	0.046	4.098	<0.001
Palearctic	-0.213	0.036	-6.004	<0.001
ExpPrey:NDVI	-0.456	0.082	-5.566	<0.001
ExpPrey:Human	0.204	0.076	2.667	0.008
NDVI:Human	-0.620	0.075	-8.218	<0.001
NDVI:Forest	0.076	0.075	1.015	0.310
ExpPrey:Indo-Malaya	0.023	0.096	0.239	0.811
ExpPrey:Nearctic	0.404	0.131	3.093	0.002
ExpPrey:Neotropics	0.042	0.064	0.653	0.514
ExpPrey:Palearctic	0.869	0.078	11.215	<0.001
Large Felids	Estimate	Std. Error	z value	P
(Intercept)	0.285	0.055	5.207	<0.001
ExpPrey	1.415	0.089	15.958	<0.001

NDVI	-0.349	0.101	-3.453	0.001
Human	-0.118	0.057	-2.059	0.039
Forest	0.132	0.072	1.843	0.065
Indo-Malaya	0.242	0.088	2.763	0.006
Nearctic	-0.597	0.089	-6.704	<0.000
Neotropics	0.035	0.082	0.420	0.674
Palaearctic	0.166	0.061	2.743	0.006
ExpPrey:NDVI	-1.433	0.135	-10.589	<0.001
ExpPrey:Human	-0.083	0.119	-0.696	0.487
NDVI:Human	-0.397	0.128	-3.111	0.002
NDVI:Forest	-0.201	0.115	-1.745	0.081
ExpPrey:Indo-Malaya	0.272	0.120	2.272	0.023
ExpPrey:Nearctic	4.098	0.397	10.314	<0.001
ExpPrey:Neotropics	0.138	0.119	1.153	0.249
ExpPrey:Palaearctic	0.608	0.105	5.765	<0.001

Small felids	Estimate	Std. Error	z value	P
(Intercept)	0.560	0.042	13.206	<0.001
ExpPrey	0.613	0.067	9.100	<0.001
NDVI	0.725	0.086	8.385	<0.001
Human	-0.108	0.046	-2.369	0.018
Forest	-1.111	0.083	-13.459	<0.000
Indo-Malaya	0.224	0.060	3.724	<0.001
Nearctic	-0.441	0.055	-7.986	<0.001
Neotropics	0.246	0.054	4.527	<0.001

Palearctic	-0.444	0.044	-10.152	<0.001
ExpPrey:NDVI	-0.414	0.101	-4.105	<0.001
ExpPrey:Human	0.256	0.092	2.771	0.006
NDVI:Human	-0.643	0.088	-7.312	<0.001
NDVI:Forest	0.906	0.104	8.684	<0.001
ExpPrey:Indo-Malaya	-0.288	0.136	-2.120	0.034
ExpPrey:Nearctic	-0.604	0.137	-4.396	<0.001
ExpPrey:Neotropics	0.029	0.077	0.385	0.701
ExpPrey:Palearctic	1.191	0.105	11.373	<0.001

Table 3: Felid mass, Felid total mammal availability, the minimum and maximum masses of species- or genera-specific primary prey, the number of which are primary prey, the proportion of primary prey that are threatened, the proportion of primary prey that are either threatened or threatened or declining, and the felid's mean resistance score to defaunation (see Eq.1 for calculation).

	Felid	Total	Min	Max		Prop.	Prop.		Prey	Decline
Felid Binomial	Mass	Mammal	Primary	Primary	No.	Primary prey	Primary prey	Mean	Listed	as a
	(kg)	Diversity	prey	prey Mass	Primary	Threatened	Threatened	Resistance to	Threat	by
			Mass	(kg)	prey	(%)	or Declining	Defaunation	IUCN	
			(kg)				(%)			
<i>Panthera tigris</i>	162.56	726.00	12.00	825.00	30	33.33	60.00	0.94	Yes	
<i>Panthera leo</i>	161.50	906.00	14.97	1417.49	72	43.06	61.11	3.97	Yes	
<i>Panthera onca</i>	100.00	1374.00	1.15	62.45	66	25.76	40.91	5.31	Yes	
<i>Panthera pardus</i>	55.00	1916.00	0.87	180.34	183	55.74	68.85	3.94	Yes	
<i>Puma concolor</i>	51.60	1671.00	0.28	420.10	364	27.75	41.21	6.02	Yes	
<i>Acinonyx jubatus</i>	46.70	686.00	1.59	213.50	58	24.14	41.38	2.83	Yes	

<i>Panthera uncia</i>	44.17	556.00	3.25	130.00	12	41.67	58.33	0.73	Yes
<i>Neofelis nebulosa</i>	20.50	606.00	0.19	180.34	175	37.71	65.14	5.59	No
<i>Neofelis diardi</i>	20.50	374.00	0.80	180.34	50	66.00	82.00	3.43	Yes
<i>Lynx lynx</i>	17.95	749.00	1.46	180.19	94	32.98	57.45	3.36	No
<i>Caracal caracal</i>	13.75	1203.00	0.04	29.50	395	8.86	20.00	7.01	No
<i>Leptailurus serval</i>	12.00	942.00	0.01	0.21	285	9.82	10.53	8.60	No
<i>Leopardus pardalis</i>	11.90	1309.00	0.01	55.51	760	13.16	23.82	11.65	No
<i>Pardofelis temminckii</i>	11.50	655.00	0.05	36.14	175	15.43	37.71	7.22	No
<i>Caracal aurata</i>	10.65	684.00	0.11	33.00	145	20.69	24.83	12.55	No
<i>Lynx pardinus</i>	9.40	78.00	1.96	1.96	1	0.00	100.00	0.00	Yes
<i>Lynx canadensis</i>	9.37	218.00	1.71	1.71	1	0.00	0.00	0.77	No
<i>Leopardus jacobita</i>	9.17	457.00	0.02	1.54	186	9.14	19.89	6.59	Yes
<i>Lynx rufus</i>	8.90	551.00	0.03	55.51	280	21.79	29.29	19.36	No
<i>Puma yagouaroundi</i>	7.87	1427.00	0.01	0.09	437	14.42	25.86	3.79	No
<i>Felis chaus</i>	7.39	790.00	0.05	0.36	162	10.49	25.31	3.64	No
<i>Felis silvestris</i>	5.50	1515.00	0.02	1.96	611	8.18	15.06	9.48	No
<i>Leopardus colocolo</i>	3.94	855.00	0.02	1.54	411	11.44	24.82	5.65	No
<i>Leopardus geoffroyi</i>	3.59	481.00	0.02	4.65	259	10.04	26.25	5.25	No
<i>Otocolobus manul</i>	3.50	527.00	0.02	8.00	240	5.00	18.75	14.20	Yes
<i>Prionailurus bengalensis</i>	3.30	1076.00	0.01	0.97	389	13.62	26.99	11.62	No
<i>Leopardus wiedii</i>	3.25	1340.00	0.01	22.80	798	14.91	25.56	12.07	No
<i>Felis margarita</i>	2.53	286.00	0.00	3.26	144	1.39	11.81	5.32	Yes
<i>Leopardus tigrinus</i>	2.25	1034.00	0.01	0.74	483	9.73	21.33	6.91	No

<i>Leopardus</i> <i>guigna</i>	2.23	65.00	0.04	0.04	2	0.00	50.00	0.50	No
<i>Prionailurus</i> <i>rubiginosus</i>	1.38	151.00	0.01	0.72	38	36.84	36.84	5.39	No
<i>Felis nigripes</i>	1.30	246.00	0.01	0.01	11	9.09	9.09	2.87	Yes

Figures

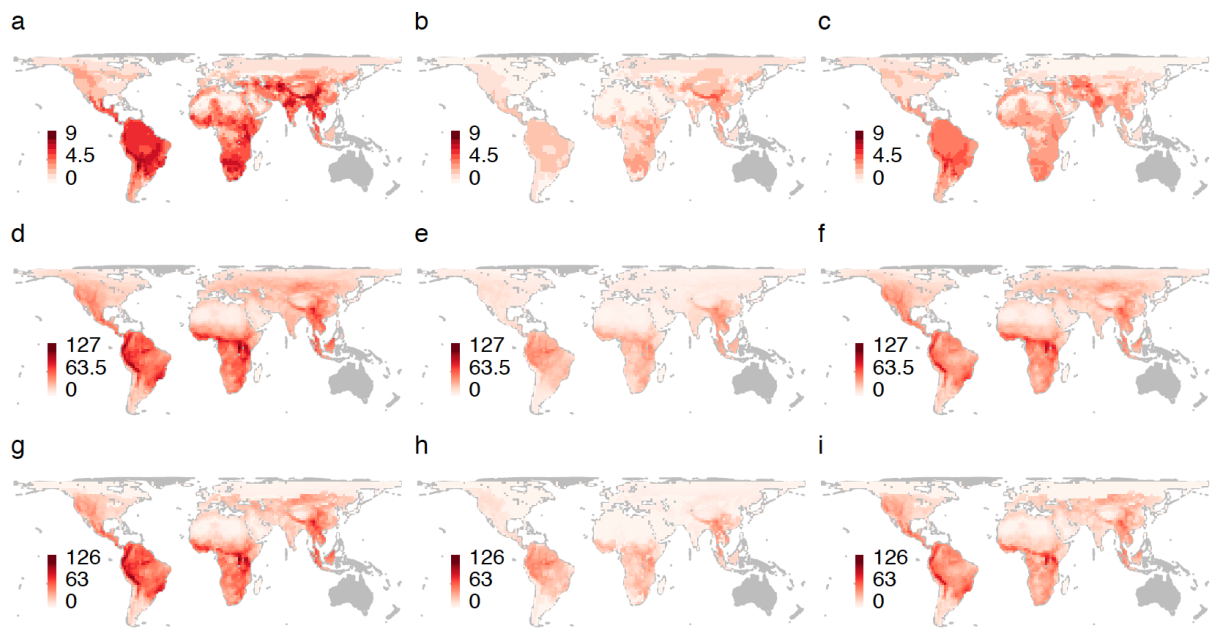


Fig. 1: Felid species-richness per grid cell for (a) all mammal-dependent felids, (b) large felids, and (c) small felids. Potential prey-richness (all felids' primary prey regardless of felid distribution) per grid cell for (d) all mammal-dependent felids, (e) large felids, and (f) small felids. Adjusted prey-richness (primary prey of the felids present in each cell) per grid cell for (g) all mammal-dependent felids, (h) large felids, and (i) small felids. The projection is Behrmann.

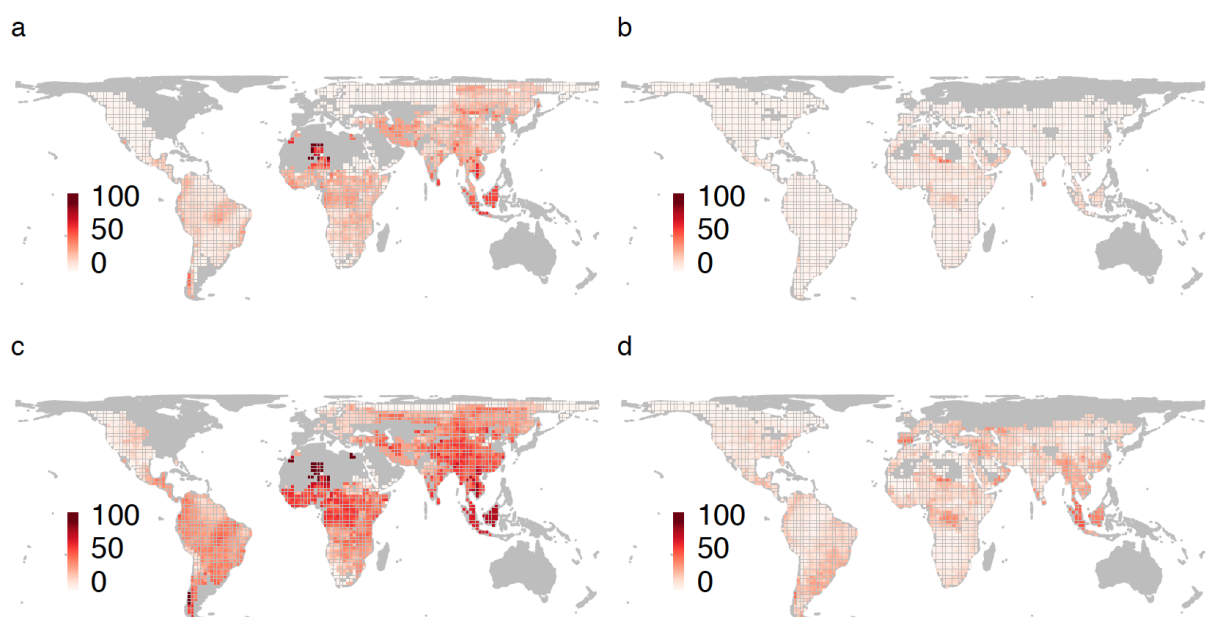


Fig. 2: The percentage of felids' adjusted primary prey-species that are threatened (a) large felids, (b) small felids, and the percentage of adjusted primary prey that are threatened or declining for (c) large felids and (d) small felids presented over a map of the world presented in grey. The projection is Behrmann.

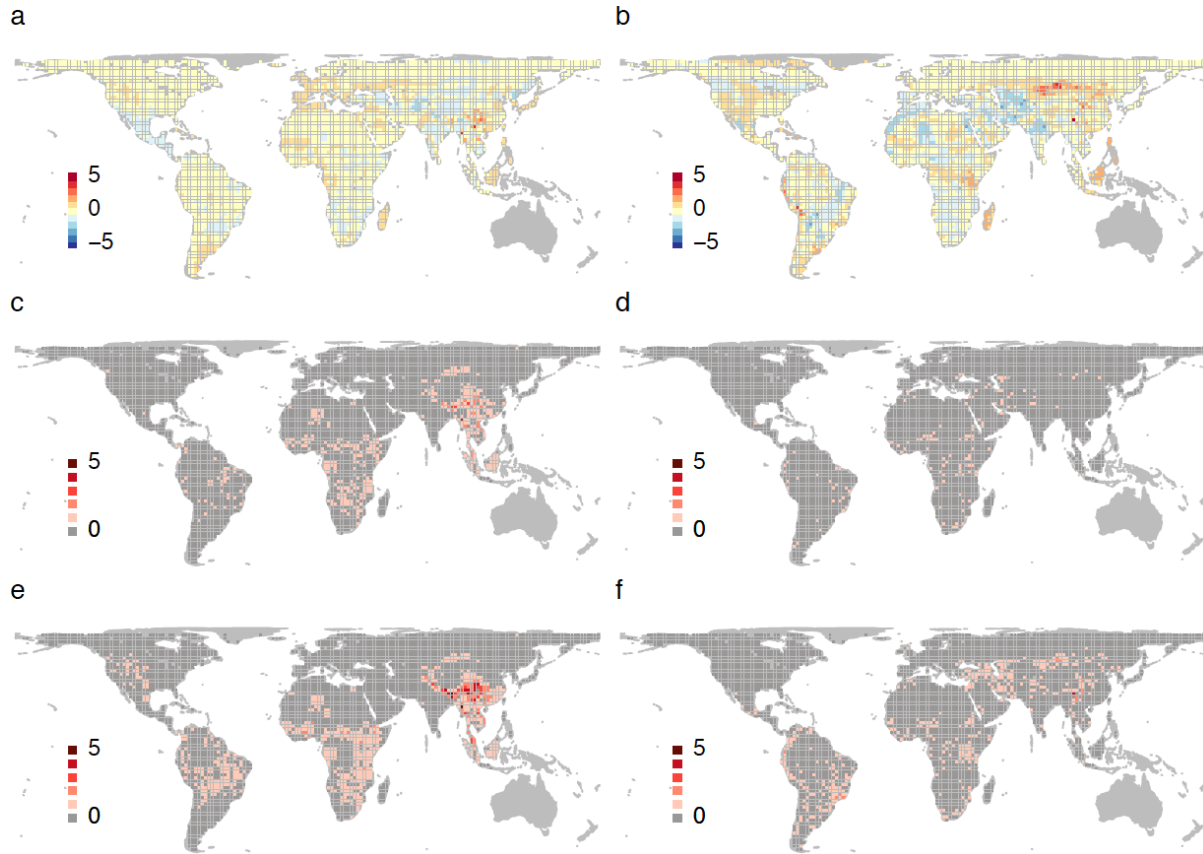


Fig. 3: Predicted felid-richness using the best General Linear Model, minus observed felid-richness for (a) large felids and (b) small felids. The number of felids predicted to be lost as the result of removing threatened mammals from the 'adjusted' primary prey-richness for (c) large felids and (d) small felids. The number of felids predicted to be lost as the result of removing threatened and/or declining mammals from the 'adjusted' primary prey-richness for (e) large felids and (f) small felids. The projection is Behrmann.

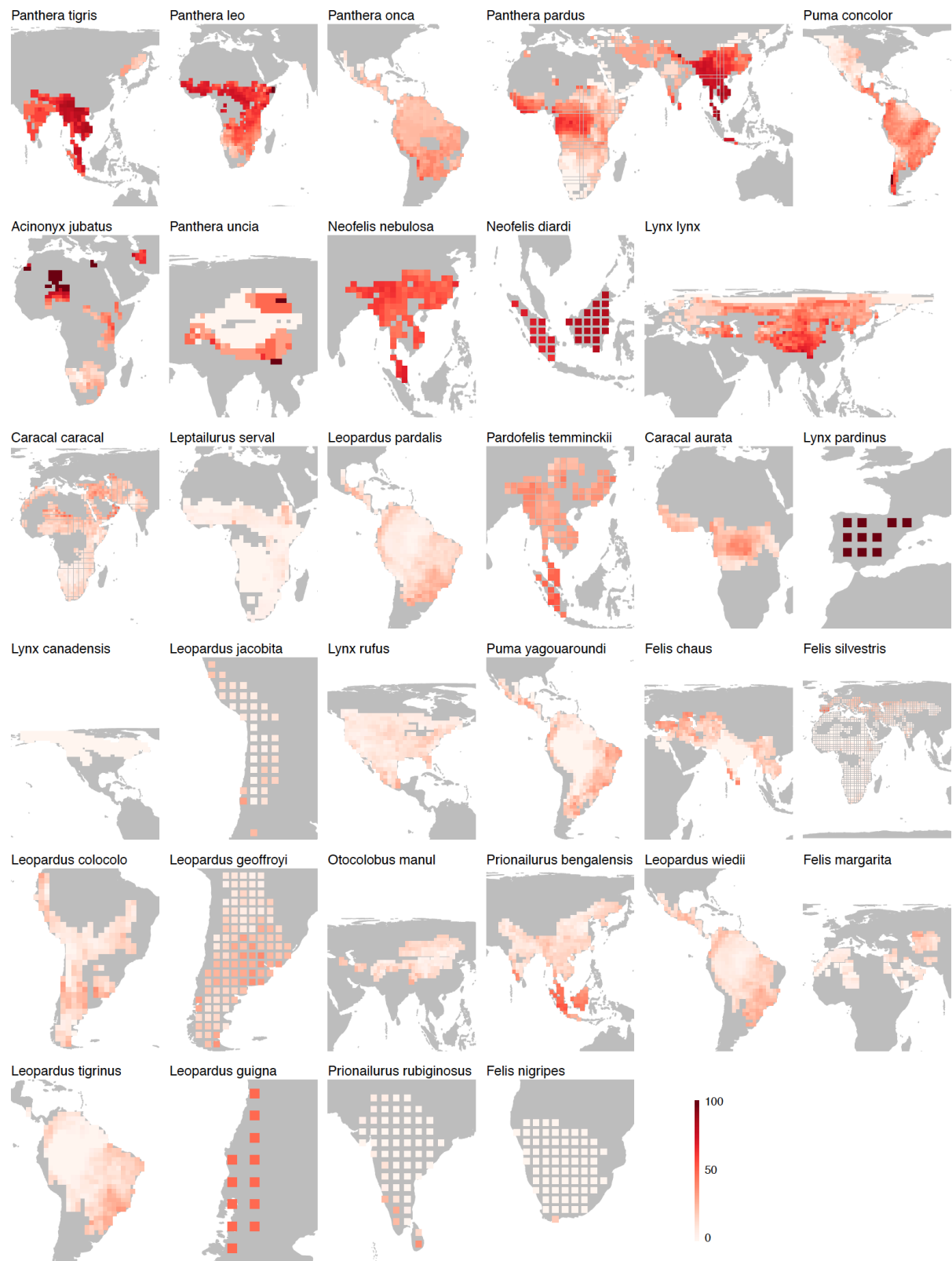


Fig. 4: The percentage of each felid's primary prey-species that are either threatened or declining in each grid cell of the felid's range. The projection is Behrmann.

Supplementary Material

Supplementary method

FelidDIET database

To answer our primary question, a dataset of felid diets (Appendix 1: FelidDIET; see Table S1 for metadata; See Fig. S1 for dataset construction methodology) was collated from the academic literature. We compiled diet data information for the 32 extant felids that primarily prey upon mammals (thus excluding *Pardofelis badia*, *Pardofelis marmorata*, *Prionailurus planiceps*, *Prionailurus viverrinus*), as identified by Kissling et al. (2014). We began by searching the International Union for Conservation of Nature's (IUCN, 2014) webpages on each felid for the species of mammal reported to be their prey. Diet data were then collected from secondary references cited by the IUCN. This revealed Sunquist and Sunquist (2002) to be a particularly important resource, and all felid diet data were extracted from this publication regardless of whether it was cited on the IUCN webpage for the felid in question or not. Diet data were then collected from all papers published between 2003-2014 recorded in the IUCN Felid Group library (<http://www.catsg.org/catsglib/index.php>) that contained 'diet' in the title, and all papers returned from a Web of Science search with one of the 32 felid binomials and 'diet' in their title, abstract or keywords. This resulted in felid diet data being collected from 176 sources that provided data from 237 individual studies (sources recorded in Sunquist and Sunquist (2002) were counted as individual studies for the latter calculation).

Prey data were recorded at species resolution where possible. Where species level diet data were not available, the highest taxonomic resolution available was used (genus, family, or order). Where common names were used, they were matched to the IUCN species lists where possible. Failing that, an internet search was made in an attempt to assign the common name to a species or taxonomic group. In total, 5918 diet records were collected, of which 5330 were recognised species or groups and came from samples large enough to be included in the analysis. For all 32 felids studied, 551 mammal species were listed as being felid prey at the species level, while a further 136 genera, 43 families and 13 orders were listed as taxonomic groups of prey-species. Quantitative (frequency of occurrence, proportion of occurrence, or proportion of biomass consumed) or qualitative (descriptions) diet data were recorded for each diet item reported. The country, region and/or site for each diet record were recorded where reported. Diet data were collected by CJS, JW, and AEH. All data entries were double-checked against the original literature by CJS.

An estimate of total diet data quality for each felid was calculated by multiplying the number of diet analysis sites by the total number of samples analysed (Table S2). A felid was considered to have Very High data quality if it scored 10,000 or more, High if it scored between 1,000 and 10,000, Poor if it scored less than 1,000 and Very Poor where no quantitative data was recorded. Twelve felids were recorded to have Very High quality data, six High, ten Poor and four Very Poor. Of the large felids, only *Neofelis nebulosa* and *N. diardi* did not score Very High data quality. Four small felids recorded Very High data quality and twelve scored Poor or Very Poor.

Geographic location data were available for 86.1% diet records at country level, 19.7% for region, and 58.7% for site-level records. Records without geographical data were typically associated with descriptive generalisations of felid diet, or taken from too large an area to be associated with a single country, region or site. The total number of samples used to assess felid diet was calculated and plotted for each country (Fig. S2a). The greatest number of samples have been reported from South Africa, particularly in Kruger National Park from

where tens of thousands lion, leopard and cheetah kills have been reported. India records the next greatest number of samples, particularly assessing tiger and leopard diets. There are generally more field diet samples available in North America, South America, Eurasia and South and East Africa. There is a noticeable dearth of samples from Central and Northern Africa, the Middle East and Indo-Malaya. Species including the clouded leopards, caracal, serval, Asian and African golden cats, wild cat, and rusty-spotted cat all occur in many countries for which no quantitative diet data were revealed in our search.

FelidDIET-Extrapolated: A database categorising the importance of every mammal within each felids range

To allow our primary research question to be answered FelidDIET was used to estimate total potential prey-richness across each felids range. The output is a dataset called FelidDIET-Extrapolated, (Appendix 2; see Table S2 for dataset metadata; see Fig. S1 for construction methodology) which lists every mammal in each felid's range and indicates whether the mammal is expected to be primary (1), secondary (2), occasional (3), or non-prey (4) for the felid in question. Primary diet species are those that are expected to form an important part of the felids diet when present. Secondary diet species are those that the felid can switch to when primary prey-species are unavailable. Occasional prey-species are those that are opportunistic predations. To construct this dataset, first, each diet item (species) or group (genera, family and order) was given an importance score based on quantitative or qualitative diet data recorded in FelidDIET. Prey items with qualitative data were assigned to prey importance categories according to key words, following (Kissling *et al.*, 2014). Words such as primary, important, and preferred were assigned to category 1. Words such as secondary, and seasonal were assigned to category 2. Words such as occasional, opportunistic, unusual were assigned to category 3. The scores associated with each word or phrase were assessed at the end for consistency between species. Where quantitative diet data were available, primary prey were those that were recorded in $\geq 20\%$ of the felid's samples, secondary prey were recorded in $< 20\%$ and $\geq 5\%$ of the felid's samples, and occasional prey occurred in $< 5\%$ of the felid's samples. A sensitivity analysis was used to assess the degree to which primary prey-richness varied by increasing the primary prey threshold to 25% and by reducing it to 15%. There was a 97.2% match between prey importance categories when increasing the threshold to 25% and a 98.6% when reducing the threshold to 15%, indicating our results are not sensitive to the threshold selected.

Two strategies were used to assign prey to their categories depending on the quality of the felid's diet data. For felids with Very High data quality, the mean of quantitative diet data was used for each prey item recorded. For felids with Very Poor, Poor or High data quality the maximum quantitative score was used. The relatively large number of sites for Very High data quality felids increases the probability of secondary prey-species being recorded as a primary prey-species. To deal with this, and because the larger number of dietary records allow it, the mean of the quantitative diet was used to assign dietary importance. This approach would be desirable for all felids to ensure the primary prey is a selective category of the most important prey-species; however, because of the limited diet data available for the other felids we assume that the diet data available for them are representative of the felid's typical primary prey. Quantitative diet data based on fewer than 20 samples were excluded from the analysis.

All mammal species associated to genera-specific diet data (i.e. all species in the genera recorded to be prey of a felid) were extracted for each felid, excluding species not found within the current range of the felid. Species- and genera- specific prey-species represent the

diet data with the greatest degree of confidence, although it will likely be an under-representation of total prey availability for each felid. These species- and genera-specific prey-species were used to determine the mass characteristics of prey (maximum and minimum prey masses) for each diet importance category (primary, secondary, occasional) for each felid as an indication of each felid's mechanical (maximum) and energetic (minimum) constraints for prey selection (Carbone *et al.*, 1999).

To estimate prey availability across each felid's range and to utilise less precise prey data, a list of species names was then extracted for diet data recorded at the resolution of family or order, excluding species that do not occur in the range of the felid. Each family- or order-specific prey-species was given the diet importance category using the same method for species- and genera-specific prey-species, however, if the mass of family- or order-specific prey-species was more than 10% greater than the maximum or more than 10% less than minimum prey mass for that category of prey, as recorded using the species- and genera-specific prey-species, the importance category was reduced accordingly. This method was used to ensure a greater degree of primary prey specificity for coarser diet data quality, representing the mechanical and energetic constraints on predator's prey selection. Finally, all mammals that occurred within the range of the felid but were not recorded as prey were identified and checked to see which of these species would have been included if a species-specific prey record had been recorded at a lower taxonomic level, i.e. genus, family or order. If the species would have been recorded to be prey under this criterion the species was matched to the closest prey-species according to phylogeny and mass.

In FelidDIET-Extrapolated, 3740 species (92.5% of all mammals that overlap the felids range) are recorded as potential prey of the felids. For the purposes of this analysis we are interested in the richness of the prey-species that primarily sustain felids. The mechanical and energetic constraints felids face mean prey opportunistically taken are not capable of sustaining them, as a result we exclude occasional prey from our analysis. Primary and secondary prey are both considered to be important to each felid, however, secondary prey are the species that felids' can utilise in the absence of their primary prey. As our purpose is to explore the impact of defaunation of prey communities we focus on the felids' primary prey-species. Collectively for all felids investigated, 2534 (62.6%) were recorded as primary prey. Of the 1511 species that were not recorded as primary prey for any of the 32 felids (excluding Carnivora and species that do not overlap the range of any felid; Table S3), 848 were from the order Chiroptera. Apart from the flying foxes, *Pteropus*, Chiroptera were only recorded as occasional prey for felids. As the only volant order they are likely to be typically functionally inaccessible to felids. To avoid Chiroptera creating strong spatial biases in felid-mammal-richness community structure all Chiroptera except for the genera *Pteropus* were removed from the analyses.

A positive correlation between log felid mass and log primary prey mass (primary prey with a taxonomic specification of species or genus) explaining 55.6% of the variation was recorded (Fig. S5a, Table S5, *GLM*: $F_{(1,1040)} = 1305$, $P = <0.001$). The strength of the relationship is reduced when including prey data recorded at family and order resolution, whereupon the model explains 34.9% of the variation (Fig. S5b, Table S6, *GLM*: $F_{(1, 7240)} = 3882$, $P = <0.001$).

To assess the implications of the differing diet data quality for each felid, species accumulation curves, maps of diet sample availability per country, and a series of maps depicting prey-richness under different measures were plotted (Fig. S2). The species

accumulation curves take into account the prey items or groups recorded in each reference as well as the maximum and minimum masses of the species- and genus-specific prey data. The accumulation curves were calculated by randomising the order references were added and calculating for each additional reference the maximum and minimum mass of species and genus specific-prey-species and the total prey-richness. The process was repeated 100 times and the median taken for maximum and minimum masses and prey-species-richness. Felid primary prey-richness is a function of the number of mammal species that are within a taxonomic group recorded to be prey of that felid that falls within the maximum and minimum mass criteria. Of the large felids (mass ≥ 15 kg), seven record fewer than 100 primary prey-species (Table 3). These felid's typically record larger prey minimum prey masses than the other three large felids. Tiger and lion in particular seem to be constrained to large-bodied primary prey, with minimum primary prey masses of 12 kg and 15 kg respectively (Table 3). Puma and clouded leopard also record Rodentia as primary prey, which results in high primary prey-richness estimates. Primates are recorded as primary prey for leopard, which, along with its very broad geographical range, again results in high total prey-richness.

Of the small felids, six were recorded to have a maximum and minimum primary prey mass range over 20 kg, while all of the other small felids had a range less than 10 kg (Table 3). Rodentia was also recorded to be a primary prey group for these six felids, ensuring each of these felids has a diverse range of primary prey. Five small felids (*Lynx pardinus*, *L. canadensis*, *L. guigna*, *P. rubiginosus*, and *Felis nigripes*) have fewer than 100 primary species (Table 3). *Lynx pardinus* and *L. canadensis* are rabbit specialists, but all of these species have relatively small ranges with relatively few mammals occurring in their range that probably accounts for the low prey-richness recorded. *Leopardus guigna* and *P. rubiginosus* have very small primary mass ranges and Poor or Very Poor data quality meaning prey-richness for these felids may be under predicted.

Data analysis

In total 18 models were analysed for each set of felids (all, large, and small). Beyond the three measures of diet richness, we identified primary productivity (NDVI), human impact, tree cover, and biogeographic realm as key predictors of felid-richness. We identified interactions between prey-richness and NDVI, prey-richness and human impact, and forest cover and NDVI as potentially important. We identified these interactions as important because we expect prey-richness to be a less important predictor of felid-richness where prey abundance or human impact is high, and the effect of forest cover to be greater in tropical environments where more mammals are arboreal.

Supplementary References

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Supplementary tables

Table S1: Variable definitions for FelidDIET

Variable name	Variable definition	Units	Storage type	Range numeric values	Categorical variables	Missing value codes
ID	Numerical identifier for the diet record	N/a	Character	1-5918	N/a	NA
FelidBinom	Binomial of the felid the diet record is for	N/a	Character	N/a	N/a	NA
PreyOrder	Taxonomic order of prey item recorded. Note the PreyOrder is only recorded for prey recorded with a Taxonomic Precision of Order.	N/a	Character	N/a	N/a	N/a
PreyFamily	Taxonomic family of prey item recorded. Note the PreyFamily is only recorded for prey recorded with a Taxonomic Precision of Family.	N/a	Character	N/a	N/a	N/a
PreyGenus	Taxonomic genus of prey item recorded. Note the PreyGenus is only recorded for prey recorded with a Taxonomic Precision of Genus or Species.	N/a	Character	N/a	N/a	N/a
PreySpecies	Species epithet of prey item recorded. Note the PreySpecies is only recorded for prey recorded with a Taxonomic Precision of Species.	N/a	Character	N/a	N/a	N/a
Prey Common Name	Common name of prey items reported by their common names.	N/a	Character	N/a	N/a	NA
Taxonomic Precision	Taxonomic level the prey item was reported at.	N/a	Character	N/a	Species, Genus, Family, Order	NA
Based On Common Name	Identifier of prey items reported by their common name	N/a	Character	0-1	N/a	NA
Prey Importance	Categorical variable of prey items importance to the felid. Note prey importance is only recorded in the table for qualitative diet data.	N/a	Character	1-4	1 = Primary, 2 = Secondary, 3 = Occasional, 4 = Non-Prey	NA
Descriptive Prey Importance	A description of the key words used in the literary source to describe the importance of the prey item to the felid.	N/a	Character	N/a	N/a	N/a
Quantitative	The proportion the	%	Character	0-100	N/a	NA

Prey Importance	recorded prey item makes up of the felids diet.					
n	The sample size of the study	N/a	Character	20-23824	N/a	NA
Country	The country the prey items was recorded	N/a	Character	N/a	N/a	NA
Region	The region the prey items was recorded	N/a	Character	N/a	N/a	NA
Site Name	The site name the prey items was recorded	N/a	Character	N/a	N/a	NA
Primary Ref	The literary reference the prey item record was collected from	N/a	Character	N/a	N/a	NA
Collection Ref	The literary reference the prey item record was collected from	N/a	Character	N/a	N/a	NA
Season	The season in which the prey item was reported to be prey in	N/a	Character	N/a	N/a	NA
Sample Source	The nature of the sample material the diet data were collected from	N/a	Character	N/a	e.g. Scat, Observation	NA
Method	The method used to calculate the importance of a prey item in the study	N/a	Character	N/a	Biomass (%), Frequency of occurrence in sample (%), Frequency of occurrence in prey (%), Meta analysis, Qualitative	NA

Table S2: Variable definitions for FelidDIET-Extrapolated

Variable name	Variable definition	Units	Storage type	Range numeric values	Categorical variables	Missing value codes
ID	Numerical identifier for the diet record.	N/a	Character	1 - 25454	N/a	NA
Felid	Binomial of the felid.	N/a	Character	N/a	N/a	NA
Prey	Binomial of the prey item.	N/a	Character	N/a	N/a	NA
PreyOrder	Taxonomic order of prey item.	N/a	Character	N/a	N/a	NA
PreyFamily	Taxonomic family of prey item.	N/a	Character	N/a	N/a	NA
PreyGenus	Taxonomic genus of prey item.	N/a	Character	N/a	N/a	NA
PreySpecies	Species epithet of prey item.	N/a	Character	N/a	N/a	NA
PreyMass	Mass of the prey-species. Source: (Faurby & Svenning, 2016).	kg	Character	0.0016 - 3940.0343	N/a	NA
DietCategory	Categorical variable of prey items importance to the felid.	N/a	Character	1 - 4	1 = Primary, 2 = Secondary, 3 = Occasional, 4 = Non-Prey	NA
DataQuality	Taxonomic level the prey item was reported at.	N/a	Character	N/a	Species, Genus, Family, Order, Extrapolated	NA

Table S3: Mammalian orders not predated as Category 1 prey by mammal-dependent felids.

Order	Number Species in Order	Proportion of order not category 1 prey
Chiroptera	861	0.98
Eulipotyphla	411	0.97
Rodentia	1922	0.06
Cetartiodactyla	226	0.13
Afrosoricida	24	1.00
Scandentia	18	1.00
Macroscelidea	17	1.00
Perissodactyla	16	0.94
Primates	308	0.05
Lagomorpha	90	0.09
Paucituberculata	6	1.00
Didelphimorphia	94	0.04
Cingulata	21	0.19
Pilosa	10	0.30
Dermoptera	2	1.00
Proboscidea	2	1.00
Diprotodontia	2	1.00
Pholidota	8	0.13
Microbiotheria	1	1.00

Table S4: Felid diet data quality based on quantitative diet data. The data quality score was calculated by multiplying the number of sites (geographic locations) by the number of samples (e.g. scats). Very High ≥ 10000 ; High ≥ 1000 & < 10000 ; Poor ≥ 0 & < 1000 ; Very Poor = 0.

Felid	No. of Sites	No. of Samples	Data Quality Score	Data Quality Assessment
<i>Panthera tigris</i>	15	5722	85830	Very High
<i>Panthera leo</i>	16	41443	663088	Very High
<i>Panthera onca</i>	10	1189	11890	Very High
<i>Panthera pardus</i>	29	31522	914138	Very High
<i>Puma concolor</i>	23	7159	164657	Very High
<i>Acinonyx jubatus</i>	10	6491	64910	Very High
<i>Panthera uncia</i>	6	2157	12942	Very High
<i>Neofelis nebulosa</i>	0	0	0	Very Poor
<i>Neofelis diardi</i>	0	0	0	Very Poor
<i>Lynx lynx</i>	5	6608	33040	Very High
<i>Caracal caracal</i>	6	1493	8958	High
<i>Leptailurus serval</i>	1	211	211	Poor
<i>Leopardus pardalis</i>	12	1203	14436	Very High
<i>Pardofelis temminckii</i>	0	0	0	Very Poor
<i>Caracal aurata</i>	1	60	60	Poor
<i>Lynx pardinus</i>	4	3370	13480	Very High
<i>Lynx canadensis</i>	2	943	1886	High
<i>Leopardus jacobita</i>	1	217	217	Poor
<i>Lynx rufus</i>	7	2851	19957	Very High
<i>Puma yagouaroundi</i>	2	147	294	Poor
<i>Felis chaus</i>	1	69	69	Poor
<i>Felis silvestris</i>	6	4566	27396	Very High
<i>Leopardus colocolo</i>	1	579	579	Poor
<i>Leopardus geoffroyi</i>	5	840	4200	High
<i>Otocolobus manul</i>	2	577	1154	High
<i>Prionailurus bengalensis</i>	7	771	5397	High
<i>Leopardus wiedii</i>	3	77	231	Poor
<i>Felis margarita</i>	1	182	182	Poor
<i>Leopardus tigrinus</i>	1	162	162	Poor
<i>Leopardus guigna</i>	1	170	170	Poor
<i>Prionailurus rubiginosus</i>	0	0	0	Very Poor
<i>Felis nigripes</i>	1	3821	3821	High

Table S5: Linear model comparing log felid mass against log prey mass (species + genera)

	Estimate	s.e.	t	p
Intercept	-4.570	0.115	-39.88	<0.001
Log primary prey mass	1.663	0.046	36.12	<0.001
R² (adj)	0.556			
F	1305 (1, 1040)			
p	<0.001			

Table S6: Linear model comparing log felid mass against log prey mass (species + genera + family + order)

	Estimate	s.e.	t	p
Intercept	-4.246	0.044	-95.73	<0.001
Log primary prey mass	1.224	0.020	62.30	<0.001
R² (adj)	0.349			
F	3882 (1, 7240)			
p	<0.001			

Supplementary figures

Please see figure at the end

Fig. S1: Flow diagram of data collection methodology to create the FelidDIET database.

Please see figure at the end

Fig. S2: Species accumulation curves and maps of the number of diet samples available per country and the proportion of diet records that are recorded to species or genus level. (a) map depicting the number of quantitative diet samples (e.g. scat or kill observations) per country for each felid. (b) map depicting the number of species- and genus-specific primary prey-species per cell. (c) map depicting the number of species-, genus-, family-, and order-specific primary prey-species per cell. (d) plot of species- and genus-specific prey-richness against species-, genus-, and family-specific prey-richness red crosses and against species-, genus-, family, and order-specific prey-richness black crosses. (e) plot of the change in minimum (black crosses) and maximum (black circles) prey mass when adding primary references. The red crosses and line is the corresponding species accumulation curve and is assigned to the secondary y-axis. The order of adding references was randomised and repeated 100 times, and the median was taken.

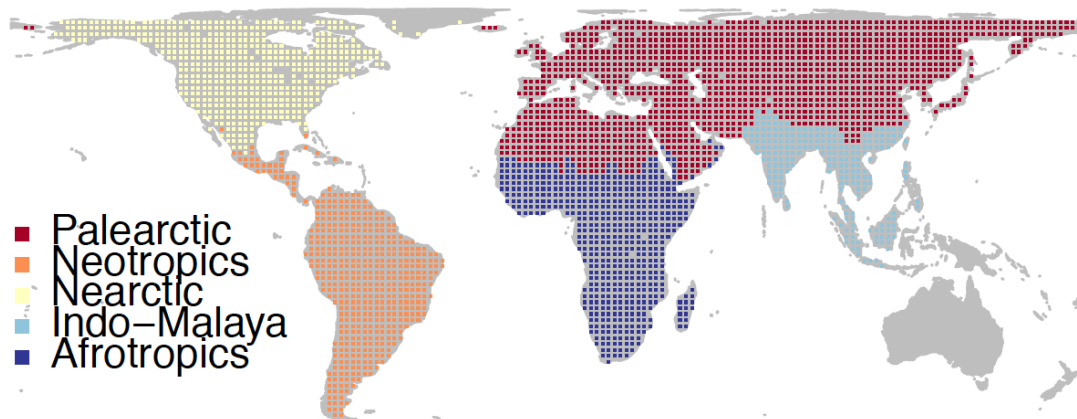


Fig. S3: Plot of the biogeographic realms (Qian, 2010) included in the analysis. The projection is Behrmann.

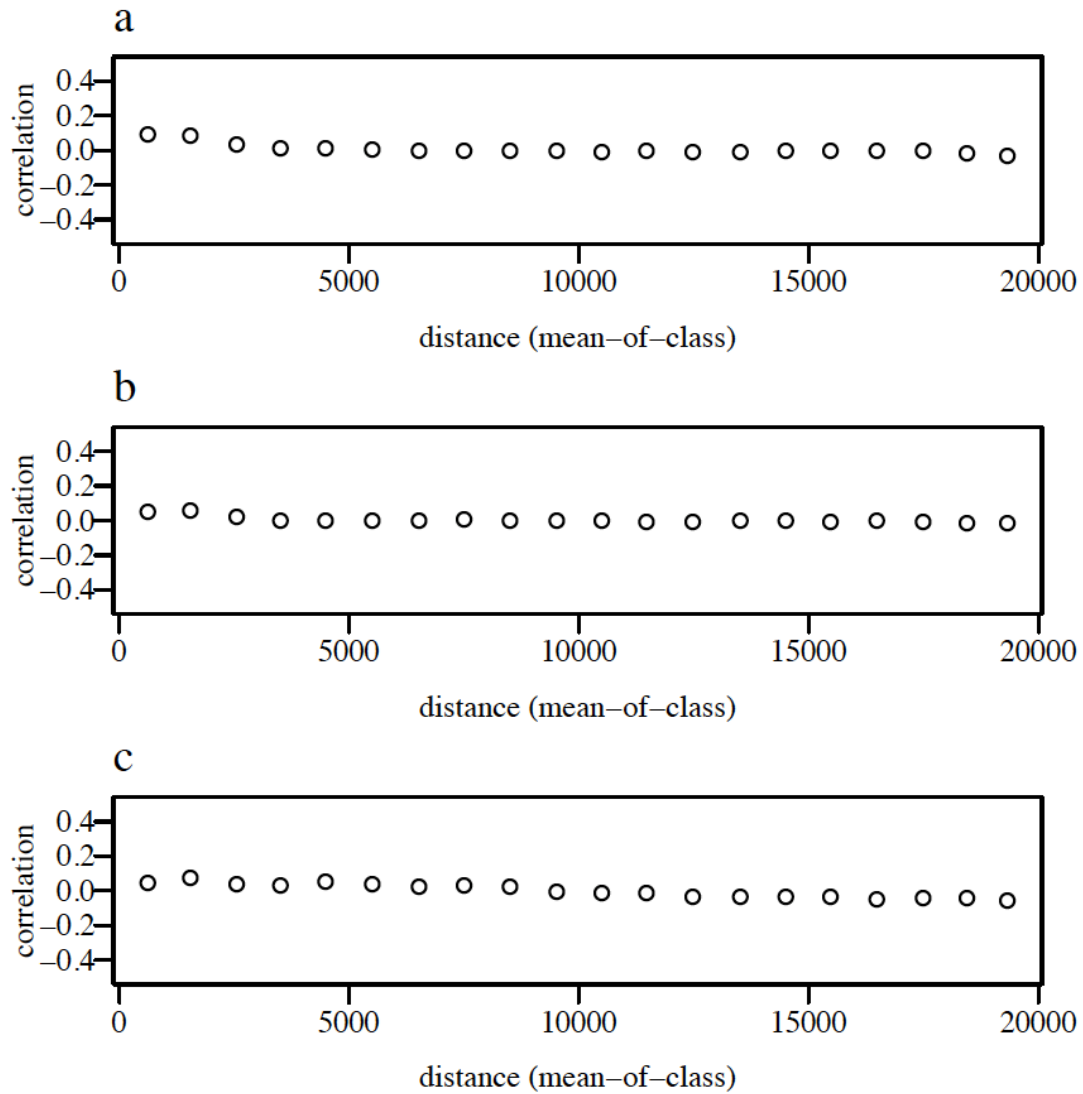


Fig. S4: Correlograms of best fit general linear regression models predicting (a) felid-richness, (b) large felid-richness, and (c) small felid-richness to assess the degree of spatial autocorrelation.

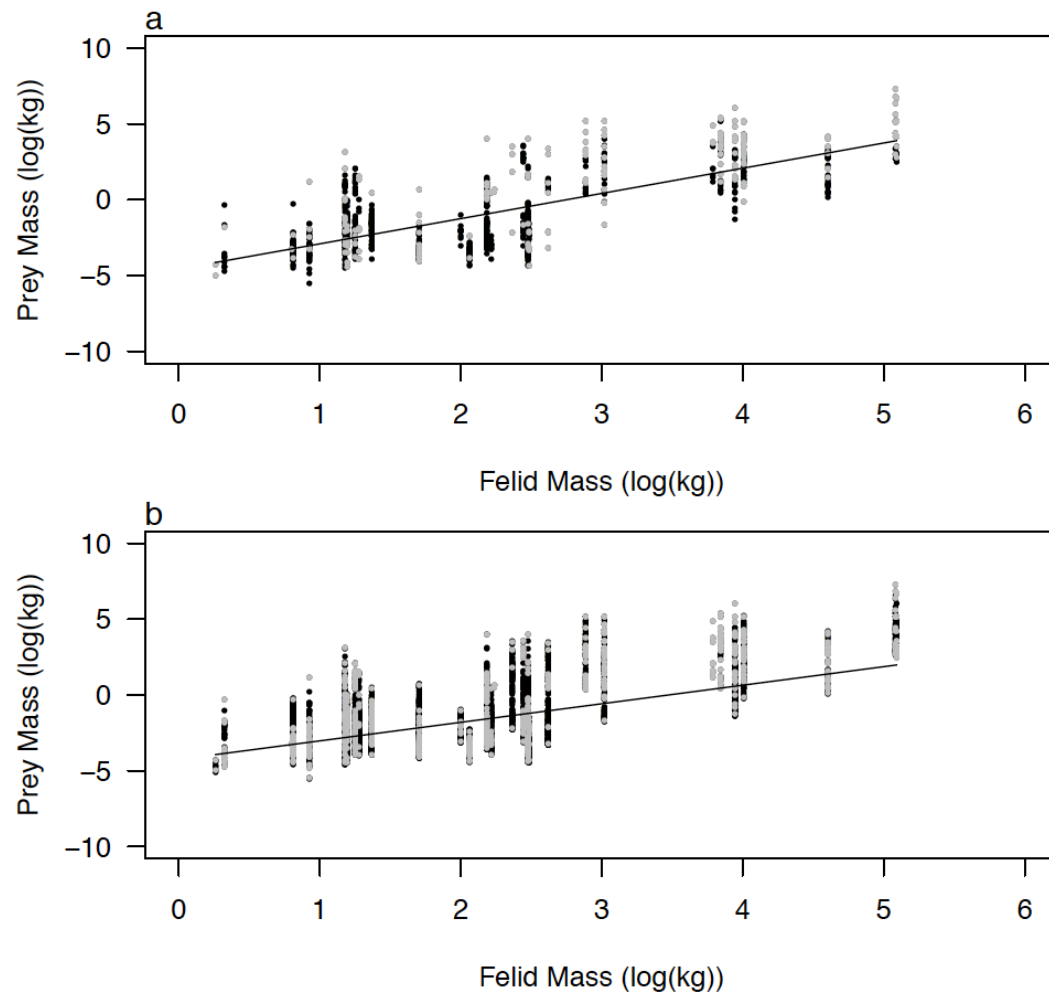


Fig. S5: Felid mass is positively correlated with primary prey mass. a) Only prey recorded at species- (grey) and genus (black) taxonomic resolution were included. b) Prey recorded at species and genus (grey), and family and order (black) taxonomic resolution were included.

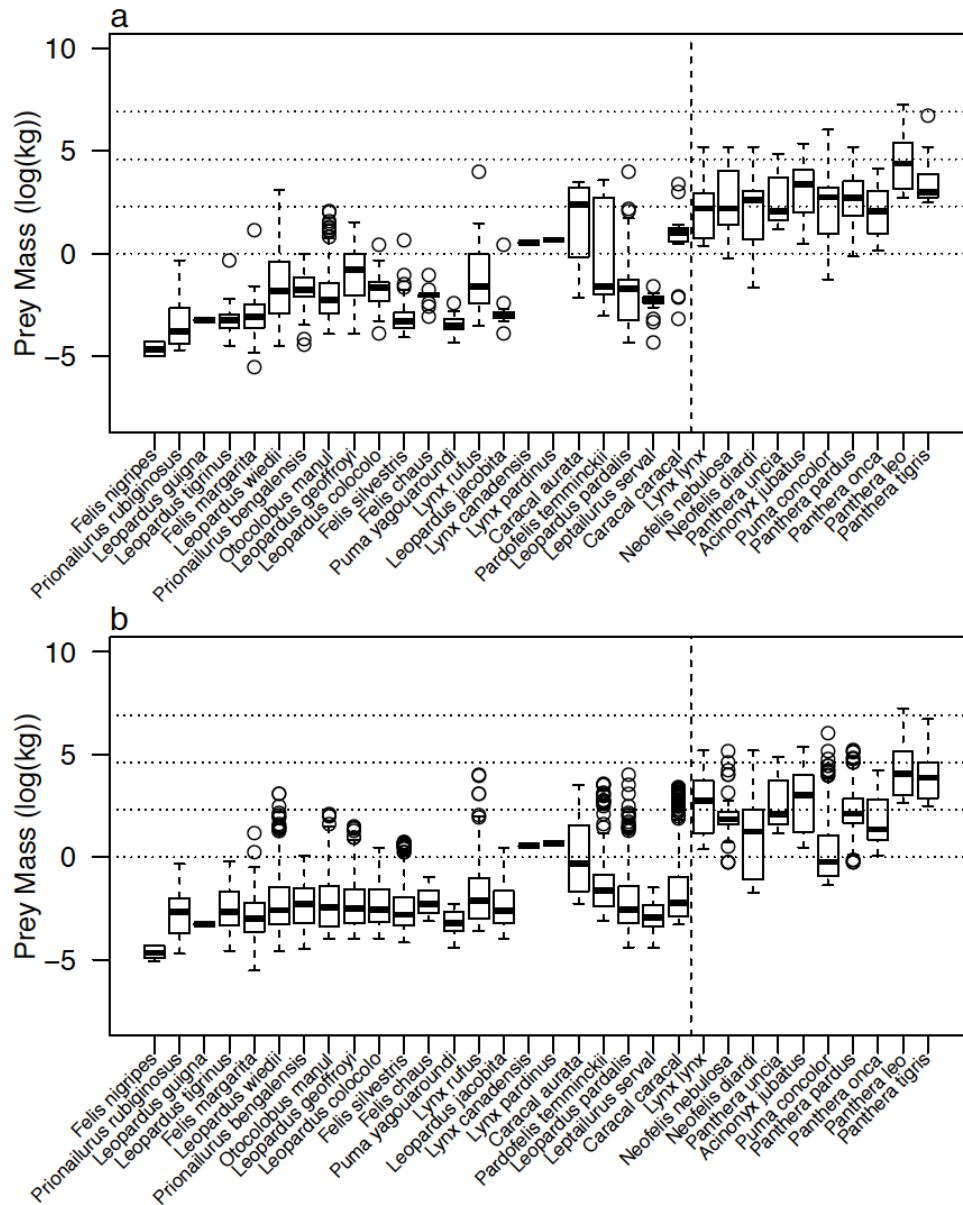


Fig. S6: Boxplot of felid primary prey masses. a) Characterisation of felid primary prey mass extracted from species and genera specific records. b): Characterisation of felid primary prey mass extracted from records from species, genus, family and order specific records. Horizontal dotted lines reflect prey masses of 1 kg, 10 kg, 100 kg and 1000 kg. The vertical dashed line indicates a divide between felids that preferentially predate large prey (to the right) and felids that preferentially predate small prey (to the left).

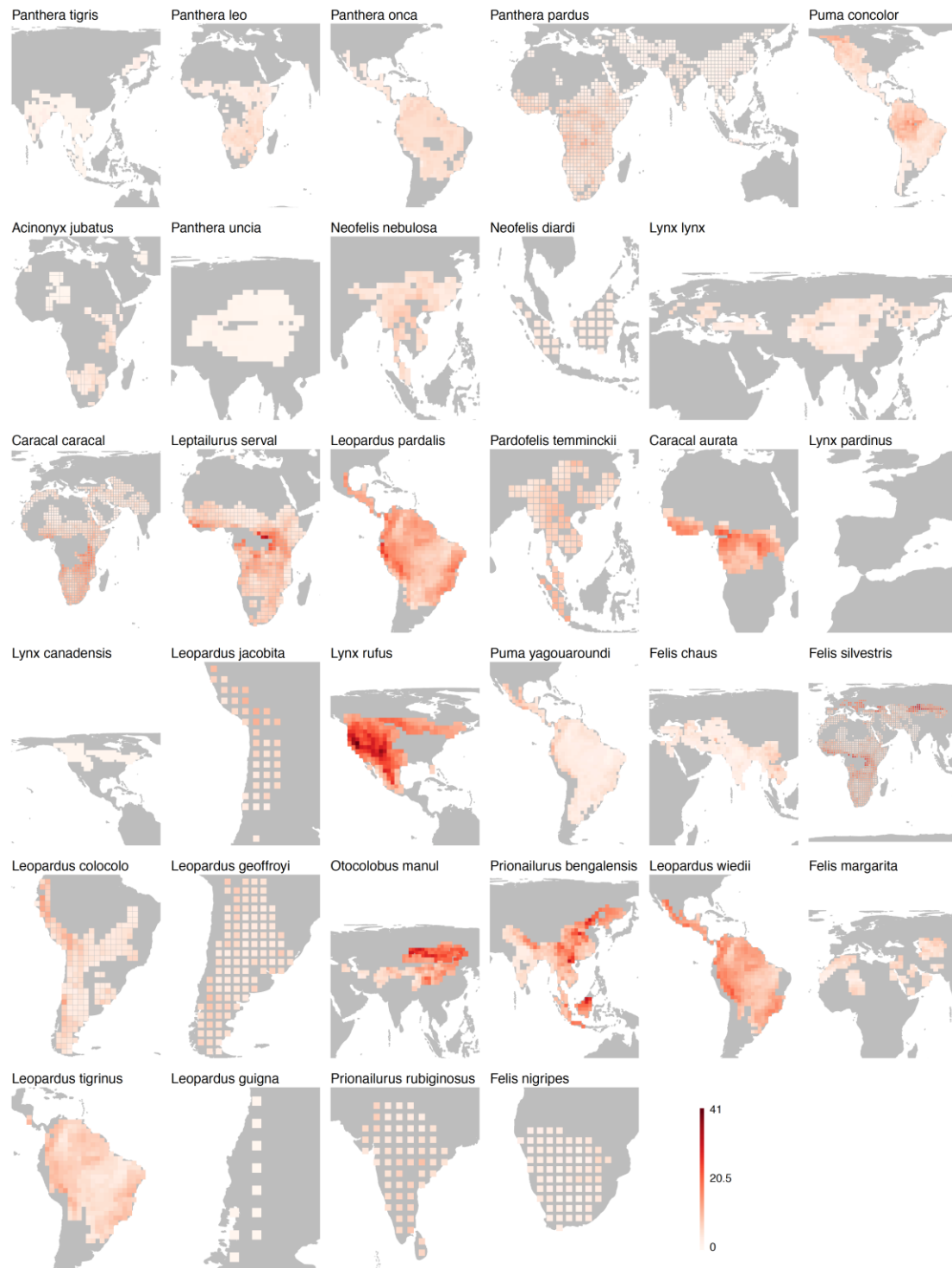


Fig. S7: Summary of threat faced by each felid to a decline in prey-richness. Each felid's resistance to defaunation was calculated for each cell by dividing the number of primary prey-species in the cell by the mean number of felids competing for these prey-species and multiplying the result by the proportion of the prey-species that are threatened or declining. Lower scores indicate a lower resistance to defaunation. The projection is Behrmann.

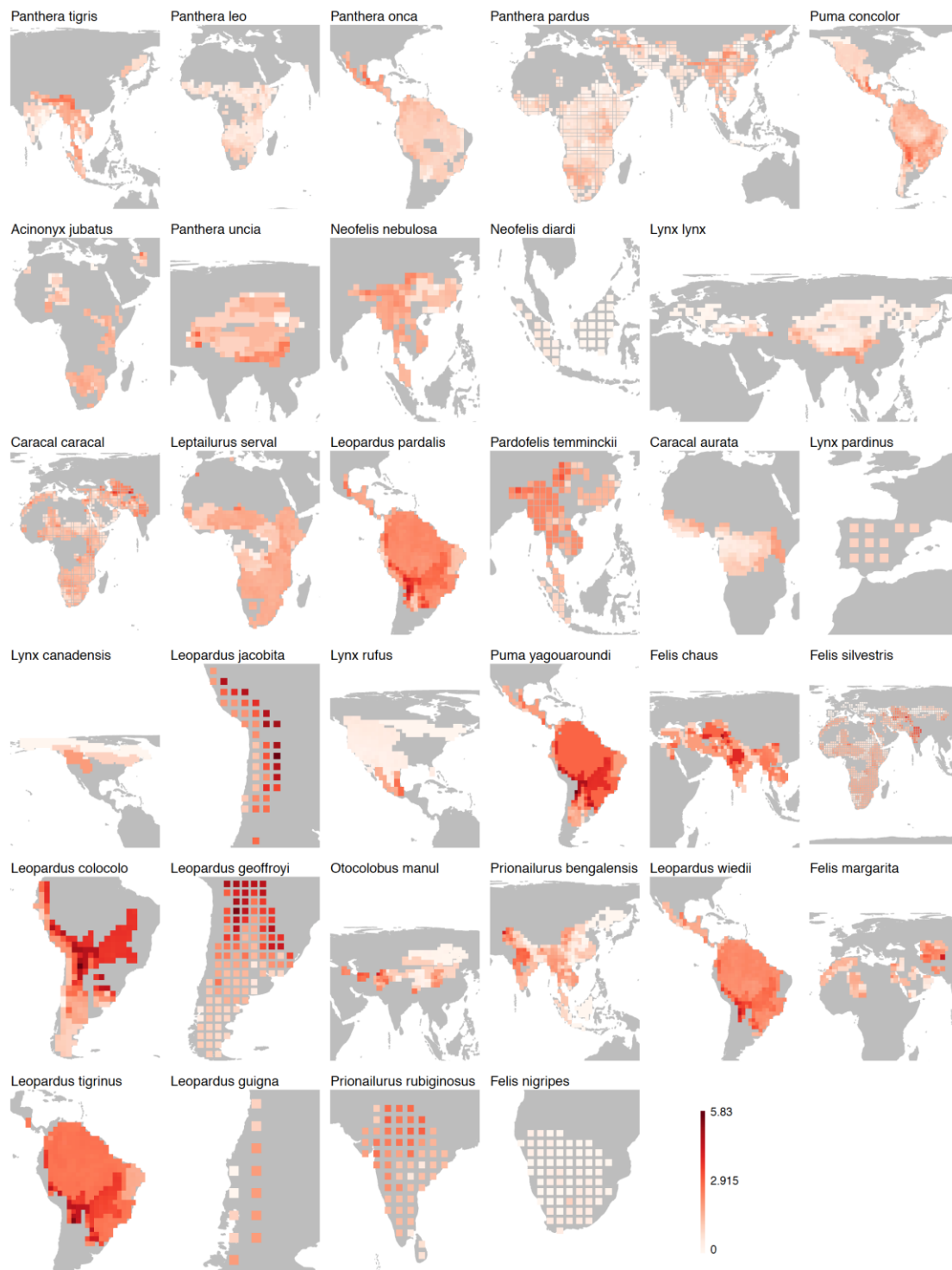


Fig. S8: The mean number of felids (large and small) that compete for each felid's primary prey-species. The projection is Behrmann.

APPENDICES

Appendix 1. FelidDIET: Raw felid diet data, collated from the scientific literature.

Appendix 2. FelidDIET-Extrapolated: Extrapolation of FelidDIET to create a dataset listing all mammals in each felid's range and their dietary importance.